

This is a rather slender species, in general proportions somewhat resembling Reeve's representation of *Bulimus Thompsoni* (Conch. Icon. pl. xxiv. fig. 158). It is moderately thin and clothed with a yellowish-olive glossy epidermis, exhibiting at short intervals oblique streaks of a darker tint and close to the suture becoming decidedly yellow, so that the upper edge of the last whorl appears to be bordered with that colour. The three uppermost volutions, which have lost the epidermis, are pale brown. All the whorls excepting the last are sculptured with spiral and oblique striæ, forming a rather fine granulation. The body-whorl is rather long and ornamented only with lines of growth which are well marked and slightly puckered at the suture. A faint band is noticeable just above the middle, and several other transverse lines parallel with it are also observable on close inspection.

This species resembles *A. simplex*, Smith, in the absence of colour-markings and in the size of the apical whorls, but differs entirely in its more elongate form. This is particularly apparent in the body-whorl and aperture.

The above description is based on a single specimen recently presented to the British Museum by Colonel J. H. Bowker. It was collected on the Drakensberg, north of Natal, at an elevation of 5000 to 6000 feet, by Mr. Henry E. Burnup, after whom I have named the species.

XLVII.—*Summary of Researches into the Anatomy and Histology of Nemertines, with Contributions to their Classification.* By Dr. OTTO BÜRGER*.

NEMERTINES used to be commonly classed with the Platyhelminthes, and thus brought into the closest relationship with the Turbellaria; only a small number of authors, among whom von Siebold † must be mentioned, placed them at an early period among the Annelids. McIntosh, however, was one of those who held this view, to which he gives expression in prefixing to the whole of his monograph the title 'The British Annelids.—Part I. Nemerteans.' Yet it is only within the last ten years that the views with regard to the proper position of the group have undergone a more extensive

* Translated from the 'Zeitschrift für wissenschaftliche Zoologie, Bd. L. Hefte 1 and 2, June 1890, pp. 248-260; whole paper, *ibid.* pp. 1-277, with ten plates and twelve woodcuts in the text.

† V. Siebold, 'Lehrbuch der vergleichenden Anatomie,' 1848.

change, owing to the recognition of a metameric arrangement in certain organs in the middle and posterior portion of the body in some more highly organized Nemertines.

To Hubrecht must be ascribed the honour of having demonstrated the existence of septa in the region of the intestinal cæca, instead of the uniform development of the gelatinous matrix, the parenchyma, in which all the organs are imbedded. This indefatigable investigator of Nemertine anatomy was likewise unremitting in his insistence on the constant relations shown in the arrangement of intestinal cæca, septa, blood-vascular loops, and, lastly, even of the proboscis-sheath.

The immediate object of all this was finally to sever the connexion between the Nemertines and the Turbellarians, and to enrol them among the Annulata. According to the old-established classification the Nemertines were completely merged in the Turbellarians, of which they were merely recognized as suborders.

Hubrecht, however, did not stop at this, but sought to establish relations between Nemertines and Vertebrates. In this direction I cannot follow him. Far-reaching speculations are permissible and justifiable only after an exhaustive study of the embryology of the form in question; and in this respect my work is completely wanting.

Yet it has seemed to me that it may be interesting to compare the various systems of organs, as we have learnt to know them in the forms we have examined, with those of the Nemertine genera not treated of in these pages, casting at the same time a passing glance in the direction of the Turbellarians and the Annelids.

Nemertines one and all possess a ciliated ectoderm. This either carries the whole of the gland-cells of the integument, and in this case rests on an almost structureless layer of connective-tissue, a so-called basement-membrane, or a portion of the gland-cells sink into the connective tissue, and we get a cutis, which is often rich in muscle-fibres. The first of these conditions is met with in all forms having a stylet in the proboscis, the Enopla, as also in *Carinella*, and, according to Hubrecht, in *Carinina*, *Carinoma*, and probably, too, in *Cephalothrix*. We find that a double layer of gland-cells, on the other hand, is characteristic of *Eupolia*, *Cerebratulus*, and *Langia*; but, from the works of McIntosh and Hubrecht, we may conclude that it is present in *Valencinia*, *Lineus*, and *Borlasia* also.

The development of a cutis is manifestly followed by highly important changes, as exemplified in the appearance

of an outer longitudinal muscular layer, of the subepithelial muscle-layers, and the formation of a muscular tissue at the cephalic extremity, where, in the case of *Carinella*, we found a parenchyma, which persists in the *Enopla* also. Moreover, we find these forms provided with cephalic glands, not present in *Carinella*, and probably likewise absent in its allies. A cephalic gland is characteristic also of the *Enopla*; and with regard to this group we may make the same observation as in the case of that to which *Eupolia*, *Cerebratulus*, &c. belong, viz. that the cephalic gland remains small in forms which, judged by the development of their nervous system, sense-organs, and cephalic grooves, must be regarded as the higher, such as *Drepanophorus* and *Amphiporus*, as also *Cerebratulus* and *Langia*; but that in *Tetrastemma*, *Prosadenoporus*, and *Geonemertes*, on the contrary, as in the more primitive *Eupolia*, it has undergone a colossal development.

The musculature of the body-wall is precisely similar in structure in the case of the first group, in which I unhesitatingly include *Carinella*, *Carinina*, and *Carinoma*—I would prefer not to come to any decision as to the position of *Cephalothrix*, although I am inclined to assign it to the first group—and in that of the third, which embraces the *Enopla*, and consists of a circular, a diagonal, and a longitudinal layer. In the second group, which includes the remaining forms unprovided with a stylet in the proboscis (*Valencinia*, *Eupolia*, *Lineus*, *Borlasia*, *Cerebratulus*, and *Langia*), we find that the musculature of the body-wall consists of a longitudinal, diagonal, circular, and longitudinal layer. The entirely different position of the diagonal muscular layer in Group II. as compared with Groups I. and III. is most remarkable.

We have recognized the inner circular muscle-layer of Group I. as not belonging to the musculature of the body-wall, and have homologized it with the dorso-ventral system which appears in the metamerized forms of Groups II. and III., and which we have derived from the circular layer in question.

None of the groups is without a system of radial muscles, the tracts of which split up the layers of the body-wall, dividing them into compartments.

In its ciliated epithelium, the manifold gland-cells thereof, and the development of the deeper system of gland-cells lying beneath the basement-membrane, the integument of the Nemertines exhibits an unmistakable resemblance to that of the Turbellarians.

The musculature of the body-wall of the Rhabdocela *

* V. Graff, 'Monographie der Turbellarien.—I. Rhabdocelida,' 1882.

displays a marked conformity with that of Groups I. and II. in that it likewise consists of circular and longitudinal layers of fibres, in addition to which, in the case of many Rhabdocœla, we also have a diagonal layer, lying between the two former. Much more complicated is the musculature of the body-wall in the Polyclads, in which, according to Lang*, as many as six layers may be present, arranged in the following order:—circular, longitudinal, diagonal, circular, diagonal, longitudinal. In this case also it is at once evident that only the internal layer of diagonal fibres has to disappear in order that we may get the arrangement of the muscle-layers found in Group II., and in *Cerebratulus* in particular.

I have alluded to the fact that the integument, and especially the ectoderm, is composed of fibrillar and gland-cells, exactly like the hypodermis of the Annelids, among which I should like to see the Gephyreans included. It remains to be added that the ectoderm of Nemertines is clothed by a cuticle, which may be provided with cilia in places. As a general rule a cutis is not present in the Annelids; yet in the case of *Sipunculus nudus*, for example, this has recently been described by Andreae†, who states that it contains pigment-masses and gland-cells. The phenomena presented by the hypodermis of the Annelids and the ectoderm of the Nemertines at the time of sexual maturity are very remarkable; in both cases the naked gland-cells swell up to a large size, almost entirely filling up the epidermis around the genital apertures (clitellum of the Earthworms, porophore of the Capitellidæ)‡. The musculature of the body-wall of the Annelids is allied to that of Groups I. and III., since it consists of a circular and a longitudinal layer. If we neglect the fact that the diagonal layer, which is stated by Andreae to lie in *Sipunculus* between these two muscle-layers, does not entirely agree in structure with that of the Nemertines, the musculature of the body-wall of a *Carinella* or a *Drepanophorus* would be essentially the same as that of the Gephyrean.

In all Nemertines the parenchyma is developed to its utmost extent, and the organs are consequently imbedded in a gelatinous tissue. In the case of Groups II. and III. this tissue is arranged in septa in the region of the mid-gut, and

* Lang, "Die Polycladen des Golfs von Neapel" (Fauna und Flora des Golfs von Neapel), Monographie, xi. 1884.

† J. Andreae, "Beiträge zur Anatomie und Histologie des *Sipunculus nudus*," Zeitschrift für wiss. Zoologie, Bd. xxxvi.

‡ Eisig, "Monographie der Capitelliden des Golfs von Neapel," Fauna und Flora des Golfs von Neapel, xvi. 1887.

at the same time a cleft appears on each side between intestine and parenchyma (*Cerebratulus marginatus* and *Drepanophorus serraticollis*). This cleft is interrupted at the points at which the extremities of the intestinal cæca come in contact with the septa, and also where those plates which include the genital sacs and the dorso-ventral muscle-bands touch the axial portion of the intestine. This cleft was pronounced by Salensky*, who determined its existence in *Monopora vivipara* and *Eupolia aurita*, to be a cœlom. Salensky finds that it is bounded by a somatic and splanchnic membrane.

The Turbellaria are devoid of cavities of this kind lying between the tissue of the body and the intestine. On the other hand, muscular septa are present, and in this respect the elongated *Gunda segmentata*† is especially worthy of notice, since in it the lateral unbranched intestinal cæca are regularly separated from one another in this way. In the other direction, however, the pronounced metameric arrangement of the septa in Nemertines leads us to the Annelids, and to the Hirudineæ in particular, in which, while a body-cavity is non-existent, muscular septa are developed.

The alimentary canal of the Nemertines exhibits two divisions, which are both histologically and morphologically well marked off from one another: these are, the fore-gut, which is devoid of cæca in all forms, but is lined by a richly glandular epithelium, and the mid-gut, which in the two last groups is provided with metamericly arranged paired evaginations, but is without glands. The intestinal cæca decrease gradually in size towards the posterior extremity of the animal, and finally we get a little short piece of intestine, straight and without glands, which we are able to distinguish as rectum, but which nevertheless in the character of its epithelial lining does not differ from the mid-gut. It is therefore doubtful whether, without referring to embryology, we are entitled to speak about a proctodæum in the case of the Nemertines. The mouth is always ventral in Groups I. and II., behind or beneath the ganglia, and opens into an expanded, bell-shaped, pharyngeal cavity—in the case of Group III. in front of the ganglia—which in its turn opens into a narrow œsophagus. The mouth does not always open independently to the exterior, but more often unites with the aperture of the proboscis-sheath. In *Monogonopora* and also in *Prosadenoporus* the œsophagus opens into the proboscis-

* Salensky, "Zur Entwicklungsgeschichte v. *Borlasia vivipara*," Biol. Centralbl. ii. Jahrg.

† A. Lang, "Der Bau von *Gunda segmentata*," Mitth. a. d. Zool. Station zu Neapel, Bd. iii. 1881.

sheath—in the latter case at some distance from its exterior aperture. The same thing very probably occurs in *Geonemertes palaensis*, only in this case the opening of the alimentary canal is carried right to the anterior extremity, so that, as a matter of fact, the apertures of mouth and proboscis coincide. In *Malacobdella*, however, the proboscis-sheath opens into a peculiar cavity, which is provided with villi, and must be regarded as a veritable pharynx. Von Kennel* would have us believe that the cavity of the proboscis-sheath opens into the mouth in *Geonemertes palaensis* also; but it appears to me, according to the figure which the author gives, that the condition is precisely the same as in *Monogonopora* and *Prosadenoporus*, that is to say that the œsophagus opens into the most anterior portion of the cavity of the proboscis-sheath. The anus, which is never absent, is always terminal.

Von Graff †, too, asserts that the proboscis-sheath in *Geonemertes chalicophora* opens into the mouth. But on referring to Taf. xxvi. fig. 7, of the work in question, we see quite clearly that the œsophagus opens into the proboscis-sheath at a considerable distance from the external aperture of the latter; it *curves distinctly upwards*, and the opening of the proboscis—of the mouth according to von Graff—is almost exactly terminal in this form, whereas it should be ventral if it were the mouth-opening. In all respects the structure presents the appearance of a prolongation of the proboscis-sheath.

In the intestine of the Nemertine we have the type of that of the Annelid. If, however, we attempt a comparison with the intestinal tract of a Turbellarian, even though we select *Gunda segmentata* for the purpose—a form distinguished by the possession of a straight unbranched intestine, which is provided with a regular series of cæcal evaginations and opens into a mouth placed at the extreme anterior end of the body—we nevertheless unavoidably fail; for the intestine of our Turbellarian, however far it may have diverged in development from the radially-branched organ of the Polyclad, in the direction of that of the Nemertine, is devoid of an anus.

According to Hubrecht ‡ and Max Müller § the proboscis

* Von Kennel, "Beiträge zur Kenntnis der Nemertinen," Arbeiten aus dem Zool. Inst. zu Würzburg, Bd. iv. 1877.

† Von Graff, "*Geonemertes chalicophora*, eine neue Land-nemertine," Morphol. Jahrb. Bd. v. 1879.

‡ Hubrecht, 'Report of the Scientific Results of the Voyage of H.M.S. 'Challenger,' 1873-1876,' Zool. vol. xix. Nemertea, 1887.

§ Max Müller, 'Observationes Anatomicæ de Vermibus quibusdam maritimis,' Berolini, 1852.

in the first two groups is provided with nematocysts (we were able to determine the presence of rhabdites only), in the third, with the exception of the parasitic *Malacobdella*, it is armed with stylets. The proboscis varies in structure in Groups I. and II., and even in the arrangement of the layers of its wall we find important variations between a *Eupolia* and a *Cerebratulus*. The proboscis of *Carinella* is composed of a circular and a strong longitudinal muscle-layer, while that of *Eupolia* shows the opposite arrangement of a longitudinal and a circular layer. In *Cerebratulus*, again, we find that the proboscis repeats the structure of the musculature of the body-wall, and we get a longitudinal, a circular, and a longitudinal muscle-layer. In *Carinella* the nerves of the proboscis adjoin the circular muscle-layer, but in the case of *Eupolia* the longitudinal layer, and in this the nerve-tissue exhibits a condition which, so far as my own experience goes, is only repeated in the proboscis of the Enopla, viz. that the nerve-mass is not adjacent to a circular muscle-layer, as it otherwise is in all our species, be they those of *Carinella*, *Eupolia*, *Cerebratulus*, *Drepanophorus*, &c., wherever we find that the nerve-mass has a constant position, whether in the form of a nerve or of a nerve-sheath. In the proboscis of *Cerebratulus* the nervous plexus, derived from the expansion of the two nerve-cords, adjoins the circular muscle-layer on the inner side. The proboscis of the Enopla exhibits a precisely similar structure, consisting of circular, longitudinal, and circular layers. The nerve-cords are imbedded in the longitudinal muscle-layer, dividing it into two sheets. The aperture of the proboscis-sheath, however, is not, as has often been assumed to be the case, terminal in position; on the contrary, it is in all forms subterminal and ventral. This is clearly expressed even in *Carinella*, where the tip of the head projects beyond the aperture of the proboscis-sheath. Another organ, however, the cephalic gland, does open terminally to the exterior.

A comparison has been suggested between the proboscis of Nemertines and the so-called proboscis of the Turbellaria Proboscidea, a terminally placed retractile and extensile sense-organ. Yves Delages* and Salensky† are among the more recent advocates of this theory. In opposition to this we may repeat once more that the aperture by which the Nemertine proboscis is extruded is by no means terminal,

* Yves Delages, "Études histologiques sur les Planaires Rhabdocœles Acœles," Arch. de Zool. expériment. et génér. sér. 2, t. iv. 1886.

† Salensky, "Bau u. Metamorphose d. Pildidioms," Zeitschr. für wiss. Zoologie, Bd. xliii. 1886.

but that the spot where the proboscis of *Convoluta Schulzii*, for example, is placed, is occupied by the cephalic gland in Nemertines.

In addition to this, the relation in which the mouth and the opening of the proboscis-sheath stand to one another, particularly as exemplified in *Malacobdella*, appears to me to be instructive, and to point to the fact that we must regard the proboscis as a species of pharyngeal apparatus—as a pharynx, which is now no longer enclosed in the pharyngeal pouch as a division of the œsophagus, but possesses a cavity of its own. The structure of the pharynx, too, is precisely similar to that of the Nemertine proboscis, consisting as it does of circular and longitudinal muscle-layers, besides radial muscles. (In the case of *Prosthiostomum sipunculus* we have the following arrangement:—longitudinal and circular layers, radial muscles, longitudinal and circular layers.) The pharynx, too, possesses gland-cells, or, at any rate, the prolongations of such cells open through its walls. The pharynx is also supplied with nerves, in the form of a nerve-sheath. The pharyngeal apparatus of the Annelids, which is styled a proboscis, is furnished with papillæ and with jaws, and is a structure which, especially in the case of the Eunicidæ, where it lies in a chamber separated from the gullet, forcibly reminds us of the Nemertine proboscis, though owing to its position, ventral to the intestine, a direct comparison between the two is impossible.

We find that the cavity of the proboscis-sheath in Nemertines increases in extent from the first group to the last. It has been regarded as equivalent to a body-cavity, and as such its development from the blastocœle proves it to be a remnant of the primitive segmentation-cavity. Hubrecht* accordingly terms this space an archicœle. The cavity of the proboscis-sheath contains free nucleated bodies, resembling blood-corpuscles; it possesses an endothelium-like lining, as is the case with the blood-vessels, in connexion with which it is supposed to have arisen.

The cavity of the proboscis-sheath may be still further increased by sac-like metamericly arranged evaginations.

The Turbellaria naturally afford us no points of comparison with reference to the cavity of the proboscis-sheath.

But what about the Annelids? I venture to put forward the following hypothesis:—While in Annelids all the organs lie in a body-cavity, in Nemertines such a cavity has only been developed to a limited extent, embracing the proboscis

* Hubrecht, "Contribution to the Embryology of the Nemertea," Q. J. M. S. vol. xxvi.

and a section of the dorsal blood-vessel. This constitutes the "rhynchocœlom," the wall of which similarly repeats the structure of the body-wall, that is, of the muscular portion thereof. The free corpuscles in the rhynchocœlom are to be compared with those of the perivisceral fluid.

We find therefore that the body of the more highly organized Nemertines possesses two cavities, which we may regard as constituting a body-cavity—the rhynchocœlom, or cavity of the proboscis-sheath, and the cleft between the intestine and the parenchyma. It must not be supposed that both these spaces are of equal value. The cellular lining of the cleft, which is in the highest degree similar to that of the genital sacs, renders it extremely probable that this cavity is a schizocœl. The rhynchocœlom, on the contrary, is a persistent segmentation-cavity (blastocœle). I must leave it to embryology to say whether one or other of these cavities is homologous with the body-cavity of the Annelids.

The blood-vascular system attains its highest development in Groups I. and II. as far as regards the elaboration of the vessels; in these groups we find, in addition to two or three longitudinal trunks, which are united together in the head and in the caudal extremity, an œsophageal blood-vascular plexus, and behind this another surrounding the cavity of the proboscis-sheath. Besides this we generally get in the second group sinus-like blood-spaces for the cephalic pits. In the three longitudinal vessels of the third group, which are united to one another by a series of metamericly arranged transverse loops, we have the nearest approach to the blood-vascular system of the higher Annelids. A blood-vascular system is wanting in the Turbellaria.

A water-vascular system is probably present in all Nemertines, with the exception of the terrestrial forms and the genus *Prosadenoporus*, in which I was not able to determine it. That of Group I. is stated to open directly into the blood-vessel. Be that as it may, it sends out cœcal tubes which enter and pierce the wall of the vessel. Most Nemertines possess only a single pair of nephridial pores; but in many forms, including *Valencinia*, *Eupolia*, *Amphiporus lactifloreus*, &c., it is stated by Oudemans* that there are a large number.

The similarity between the excretory system of the Nemertines and that of the Turbellarians is unmistakable, especially if it should be more generally found, as Silliman † claims for

* Oudemans, "The Circulatory and Nephridial Apparatus of the Nemertea," Q. J. M. S. vol. xix. n. s. 1885.

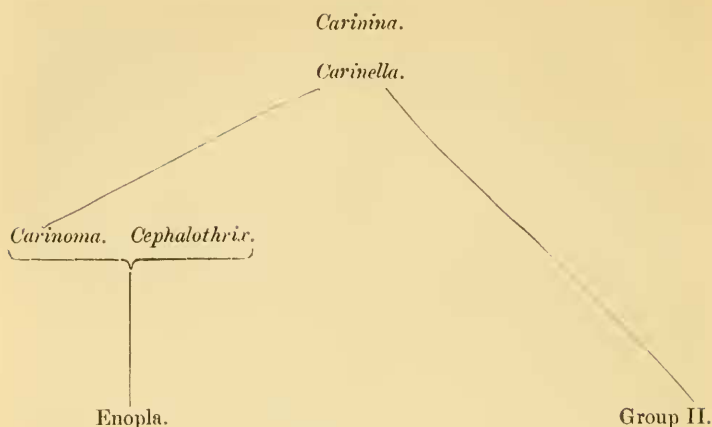
† Silliman, "Beobachtung über Süsswasserturbellarien Nordamerikas," Zeitschr. für wiss. Zoologie, Bd. xli. 1885.

Tetrastemma aquarum dulcium, that the excretory vessels of Nemertines are provided with flame-cells.

Yet we are by no means debarred from a comparison with the Annelids, even as regards the nephridial system, if we bethink ourselves of *Lanice conchilega*, that remarkable Terebellid in which four nephridia are united together on each side by a longitudinal vessel. In this connexion it is of the utmost importance to ascertain whether the forms possessing a number of excretory channels exhibit a metameric arrangement of the nephridiopores. In all probability the peculiar line of development followed by the excretory apparatus of the Annelids has been influenced by the large size of the body-cavity found in these forms.

As regards the nervous system, if we start from the lowest forms of the first group and continue our investigations through the other two, we meet with unmistakable evidence of a progressive development; and this not only in the primitive or more complicated composition of the nervous system itself, but also in its varying position, which passes from the epithelial, as described by Hubrecht for the nervous system of *Carinina*, through the intermuscular stage, until finally we find the nervous system lying entirely within the muscle-layers (infra-muscular). According to Hubrecht the most widely different stages in the progressive passage of the nervous system from the exterior towards the interior of the body is found in representatives of Group I. What is in all probability to a certain extent a resting-stage is reached when we find the nervous system situated outside the circular muscle-layer, but lying immediately upon it. I gather from the works of M'Intosh, Hubrecht, and Oudemans, that this occurs in all forms belonging to Group II. But a transition from this position to the infra-muscular one found in the Enopla is not known in this group. In order to trace this transition we have, indeed, to go back to Group I., and, according to the description and figure given by Hubrecht*, we find it in *Carinoma* and *Cephalothrix*. It is therefore from these forms, judging by the position of the lateral nerve-cords, that the Enopla are to be derived; but the genera of the second group can only have sprung from a form in which the lateral cords are still outside the circular muscle-layer. We may therefore represent the affinities thus:—

* Hubrecht, *op. cit.* tab. xi.



The central nervous system is divided into a brain and lateral cords. In addition to the swollen anterior portion of the lateral cords, which forms the ventral ganglia, the brain always shows traces of a pair of dorsal ganglia, which, in the highest forms, far exceed the ventral ganglia in size, while the degree to which they are developed appears to depend to a certain extent on the development of the lateral organs. This is proved by the most primitive forms, in which both lateral organs and dorsal ganglia are of simple structure and small size. In the higher forms, however, in which the lateral pits are reduced in size, as we have found to be the case in *Prosadenoporus*, the dorsal ganglia by no means undergo a corresponding reduction. The ganglia of the brain are united by a dorsal commissure, which passes above the rhynchodæum in *Carinella* and above the rhynchocœlom in *Cerebratulus* and *Drepanophorus*. A ventral commissure passes below the rhynchocœlom and in the *Enopla* lies upon the fore-gut. The position of the brain is consequently by no means absolutely constant even in this respect. Many Nemertines have been shown to possess an anal commissure connecting the two nerve-cords. The central nervous system possesses a variously constituted sheath of ganglion-cells, which differ exceedingly in form, according to the particular region of the brain, and are eminently characteristic of the various regions. The brain and lateral nerve-cords of certain representatives of Group II. (*Cerebratulus* and *Langia*) possess neurochord-cells and branched neurochords, which traverse the central substance of the lateral cords. Representatives of Group III. (*Drepanophorus* and *Prosadenoporus*)

possess only *one pair* of neurochord-cells, which belong to the brain, and only a single pair of unbranched neurochords, which run through the brain and the lateral cords.

The entire mass of the central nervous system is enveloped in a neurilemma. The fibrillar central substance of the lateral cords in all cases, and throughout Group II. that of the brain as well, is also enclosed in an inner neurilemma and sharply marked off from the coat of ganglion-cells.

The peripheral nervous system is represented by nerves and nerve-sheaths. Nerves supply the cephalic extremity, the eyes, and the lateral pits. A pair of nerves, which arise from the ventral ganglion, runs back to the œsophagus; a precisely analogous pair, springing from the ventral commissure, supplies the proboscis in Groups I. and II. In Group III. the proboscis is innervated by means of numerous stems, arising from the brain. In some species of the first group, and in all those of the third, the lateral organs are united by nerves to the dorsal ganglia. In all the groups the lateral cords give off nerves, which are arranged metamericly in Groups II. and III. In *Carinina* the nerve-sheath assumes an epithelial position, in accordance with the situation of the lateral cords; in the other genera of this group the sheath is subepithelial. In Group II. the nerve-sheath is generally situated outside the circular muscle-layer, but it may occur within it, as in *Langia* and *Cerebratulus*. In Group III. nerve-sheaths are not found. The nerve-sheaths are characterized by the presence of a median dorsal nerve, which runs through them in the longitudinal axis of the body. This nerve also persists in Group III., only in this case it maintains an intermuscular position, above the circular muscle-layer. A second and smaller nerve of this kind, lying within the circular muscle-layer, is characteristic of the first two groups only.

In close connexion with the nervous system come the sense-organs—the subepithelial eyes (the pigment-cups of which are directed outwards), the lateral organs, the accessory lateral grooves lined with columnar epithelium (*Drepanophorus*), and the terminal cephalic grooves (*Cerebratulus*).

The lateral organs are placed in the same position as the brain, and in a portion of the genera belonging to the first group and in all those of the second and third they fuse with the dorsal ganglion, behind which they always lie. In the Enopla they occupy an independent position, being connected with the upper ganglion by nerves only, and generally lying to the side of it, though they may occupy a position in front of it, towards the cephalic extremity. As special formations

of the body-wall we have the lateral indentations known as cephalic pits in the majority of the representatives of Group II.; these supply the place of a canal in bringing the lateral organs into communication with the outer world. We have yet to mention the existence of a pair of lateral organs in the neighbourhood of the nephridio-pores of *Carinella*.

While the Nemertines, owing to their plexus-like epithelial and subepithelial nervous layers, give grounds even for a reference to the Cœlenterates (a vista opened up by Hubrecht), nevertheless the central nervous system shows so high a degree of development, in the stoutness of its central substance, of its ganglionic coat (so widely and so sharply differentiated from it), and of the twofold membranous and fibrillar elements of its sheath, that it equals the Annelids in this respect. The appearance of a second sheath surrounding the central substance is of especial importance. An inner neurilemma of this kind, which interposes itself between the coat of ganglion-cells and the fibrillar substance, has been identified and described by Hermann* in *Hirudo* also. The tissue, however, which has been styled by many authors an inner neurilemma, does not correspond to the inner neurilemma of Nemertines. For the term has been applied to the finely fibrillar elements of the sheath of the ganglion-cells (Nansen †), or to a membranous sheath which surrounds the nervous elements, ganglion-cells, and central substance of the ventral cord of certain Annelids, and which, as an inner neurilemma, has been contrasted with an outer one, which envelops an intermediate mass lying between the two membranes (Leydig ‡, Andreae §).

In other respects the connexions which can be made out between the brain of Nemertines and that of Annelids are many in number. I may instance in particular the fact which has lately been more and more insisted upon, viz. that the ganglionic coat consists almost exclusively of unipolar ganglion-cells, and lastly, but by no means least, the occurrence in Nemertines also of neurochord-cells and neurochords.

Whether we are justified in placing the brain of Nemertines absolutely on a level with that of Annelids appears to me to be a question which must be postponed for the present on embryological grounds. Salensky arrives at the following

* Hermann, 'Das Centralnervensystem von *Hirudo medicinalis*.' München, 1875.

† Nansen, "Anatomie u. Histologie des Nervensystems der Myzostomen," *Jenaische Zeitschr.* 1887.

‡ F. Leydig, 'Tafeln zur vergl. Anatomie,' Tübingen, 1864, i. fig. 9.

§ J. Andreae, "Beiträge zur Anatomie und Histologie des *Sipunculus nudus*," *Zeitschr. für wiss. Zoologie*, Bd. xxxvi.

conclusions :—The cerebral ganglia of Nemertines and Annelids are homologous ; the ventral commissure of the Nemertine brain corresponds to that which connects the two halves of the Annelid brain ; the dorsal commissure of Nemertines is a structure *sui generis* and has no homologue in the case of the Annelids ; the œsophageal commissure of the Annelids corresponds to the lateral nerves of Nemertines.

The author draws the last inference from the fact that the Nemertine brain, which arises as an ectodermal thickening on each side of the proboscis-invagination, is prolonged posteriorly into the lateral cords. Nevertheless it is not proved that this brain is exactly the homologue of that of the Annelids, which always includes a portion of the larval apical plate ; whereas in the *Pilidium*, on the contrary, the apical plate is thrown off. In any case I am inclined to compare the lateral cords of Nemertines with the ventral cord of the Annelids (the arrangement of the nerves which pass off from the cords makes the comparison justifiable), without further discussing the question whether the Nemertine brain is to be regarded merely as an expansion of the lateral cords, or as a special formation in the same sense as the brain of the Annelid.

The grounds on which we might institute a comparison with the central nervous system of Turbellarians appear to me to be of so general a nature that they must recede into the background when contrasted with the resemblances between the Nemertine and the Annelid nervous systems.

The eyes of Nemertines, on the other hand, may be shortly characterized as Turbellarian eyes.

An agreement in the mode of origin of the lateral organs of Nemertines and the ciliated pits of certain Rhabdocœla (*Microstomæ*) has already been pointed out by Dewoletzky *, who was also successful in proving the occurrence of similar structures in the case of the Annelids. To this end the author instances Lovén's larva which is provided with ciliated pits, the larva of *Sipunculus*, and also *Ctenodrilus*, in which v. Kennel † found cephalic pits, corresponding as it were to the lateral organs of Nemertines. The similarity between the lateral organs of Nemertines and the ciliated organs of the Capitellidæ has been demonstrated by Eising also.

I will not attempt to find the homologues of the second pair of lateral organs of the species of *Carinella* in the

* Dewoletzky, "Das Seitenorgan der Nemertinen," Arbeiten aus dem zool. Inst. zu Wien, Bd. vii. 1886.

† V. Kennel, "Ueber *Ctenodrilus pardalis*," Arbeiten aus dem zool. Institut zu Würzburg, Bd. v. 1882.

Annelids—though in them only, and not in the Turbellaria, would it be possible to discover them. I will merely draw attention to the fact that with the appearance of this second pair we find that a lateral line appears in the Nemertines as the bearer of sense-organs, precisely as we find it in the Annelids.

The genital products are either formed directly in the parenchyma, in which case a membrane forms round them, constituting a sac, or else they arise in the walls of sacs which alternate with the intestinal cæca. Before maturity is reached a duct is formed, one from each sac. In the non-metamerized forms the first of these methods appears to prevail (*Carinella*), in the metamerized forms the latter (*Cerebratulus*, *Drepanophorus*). Moreover in these forms, as in *Prosadenoporus*, *Geonemertes*, and many others, several genital sacs are situated between a single pair of intestinal cæca, and we consequently find several genital pores in one metamere. Nemertines are not all of separate sexes: the terrestrial and allied forms, *e. g.* the Prosadenoporids, are hermaphrodite. Hermaphrodite forms are also found among the Tetra-stemmids, which are closely allied to the Prosadenoporids. *Prosorhochmus* and *Monopora* are stated to be viviparous.

The extraordinarily complicated genital organs of the Turbellaria exclude any comparison with those of Nemertines.

But even as regards the genital organs of the Polychæte Annelids, it is only in their simplicity that those of the Nemertines agree.

Shortly stated, the conclusion we deduce from the considerations which we have discussed in the above pages amounts to this:—That in many respects the organization of Nemertines exhibits an affinity with that of the Turbellaria, but that on the whole this is put into the shade by the general Annelid-like structure of the animals which we have been considering.

If we merely observe the living flat Nemertine crawling in its mucus, and compare it with a Polychæte or an Oligochæte, the metamerism of which is exhibited externally by means of rings and the arrangement of bundles of setæ, we find but little difficulty in persuading ourselves to follow our predecessors in the field of natural history and in agreeing with the place they assigned to these worms in their classifications—so long, that is, as we are compelled to work with the same appliances as they had. To-day, however, when methods and microscopy have overcome untold difficulties

which they had to contend against, we may judge an individual by its external appearance in the last resort only; we determine its systematic position far rather from its internal organization, as displayed to us by means of anatomy and histology, and above all from its embryology.

The latter lead us to the conclusion that Nemertines have probably been derived from Turbellarian-like forms, but that after following a line of development over which the Annelids had already passed, they diverged from it again in a direction of their own.

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XLVIII.—*On the Fate of the Quadrate in Mammals.*

By R. BROOM, M.B., C.M., B.Sc.

ONE of the most troublesome points in the study of the descent of the Mammalia is the explanation of the changes which have taken place in the structure of the lower jaw and in its mode of articulation with the skull. In Amphibians and Reptiles the lower jaw is invariably made up of a number of pieces and articulates with the skull by means of the quadrate. In Mammals the jaw is apparently a single bone articulating with the squamosal. What we have therefore to explain is, What has become of the quadrate and how has the jaw become simplified? In the present paper I shall only deal with the fate of the quadrate.

Hitherto the majority of comparative anatomists, chiefly from the study of the early condition of the visceral arches, have agreed in finding the homologue of the quadrate in one or other of the auditory ossicles. Gegenbaur, Kölliker, Wiedersheim, and Reichert find its representative in the incus, while Huxley looks upon the malleus as its equivalent. Parker, who has done more than any one else to elucidate the development of the skull, after for many years holding the same view as Huxley, ultimately came to regard the incus as the Mammalian quadrate.

That the quadrate of the Amphibian or Reptilian ancestors of the Mammals should gradually move back from the articulation of the jaw and degenerate into one of the auditory ossicles is improbable; and there is little doubt but that the view has been founded on a misinterpretation of the morpho-